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Some features of qollen-formation in the Cucurbitaceae *

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(WITH PLATES 17–21)

Studies in the development and differentiation of the anther have been frequent in recent years, and in this line we may cite the researches of Gager,[9] Rosenberg,[22] Merrell,[15] and others. In all cases the primordium of the stamen appears as a slight elevation of the tissue which later becomes outwardly differentiated into its characteristic form and inwardly into spores, tapetum, endothecium, etc. Galinski [10] found that in certain of the grasses (*Secale, Triticum*) the anther-wall became differentiated into four layers, epidermal, fibrous, degenerating, and tapetal, and that the original pollen-mother-cells may divide several times. In *Zostera* as described by Rosenberg,[22] the elongated archesporial cells cut off from their ends the cells which form the tapetum. But in *Asclepias*,[9] *Silphium*,[15] and a majority of seed-plants, the immediate hypodermal layer has been shown to divide by periclinal walls to form the primary tapetal and primary sporogenous cells, the latter in some cases undergoing repeated divisions. But in the development of pollen, interest has centered chiefly in the mitotic features exhibited during the division of the pollen-mother-cells. Among these the origin of the spindle and the reduction and behavior of the chromosomes have received most attention. The results of these numerous studies have been well summed up by Davis,[7] and Coulter and Chamberlain,[6] and space will not be taken here for a similar task.

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But few plants of the *Cucurbitaceae* have received attention from this point of view. Mirbel [16] studied the development of the anther of *Cucurbita Pepo* and demonstrated the principal facts of the process. In small buds 2 mm. long he found no trace of the locules, but in a slightly later stage he was able to discern the spore-mother-cells and the tapetum. His figures of this condition represent the anther-wall, composed of four layers of cells under the epidermis including the tapetum. In buds 3 or 4 mm. long an additional layer of cells was detected in the anther wall. The development of the pollen-mother-cells, the formation of the tetrads, and the differentiation of the pollen-grain are well described and figured.

Naegeli [19] described certain features in the formation of pollen in *Cucurbita* and in *Bryonia dioica*. He seems to have observed the first division of the microspore-nucleus in *Cucurbita* but not to have interpreted correctly what he saw. He discusses more at length the differentiation of the exine and the behavior of the intine upon the germination of the grain.

To Warming,[25] however, we are indebted for an accurate study of the development of the anthers of *Bryonia alba* and *Cyclanthera pedata*. In both these cases the first periblem layer of the anther divides by periclinal walls. From the outer cells thus formed is developed the anther-wall by succeeding periclinal divisions, and the inner cells become the archesporium. In *Bryonia* the archesporium is a single layer of cells which later forms a mass of spore-mother-cells. Warming says that, as seen in transverse section, the pollen-mother-cells form one to several rows in each angle of the anther. Not all the cells cut off toward the inner side in the division of the hypodermal cell become mother-cells, and sometimes those that do become mother-cells do not divide again until the formation of the tetrads. In *Cyclanthera* the inner cells resulting from the division of the first periblem layer as a rule do not divide again but form mother-cells by growth.

Thus the evidence indicates that in these plants the usual order of development of sporogenous tissue in seed plants is adhered to, but the subsequent history of the archesporium may vary, as it appears at present, in accordance with the form and structure of the anther, in some cases the original archesporial

cells remaining undivided, in others giving rise to a considerable mass of pollen-mother-cells.

In this study attention has been given to the development of the pollen in three species of the *Cucurbitaceae* representing as many genera. The forms studied are *Fevillea cordifolia* L., *Micrampelis lobata* (Michx.) Greene, and *Cyclanthera explodens* Naud.

In *Fevillea* at the time when the anther begins to form the archesporium appears. At this time the anthers are rounded bodies, more or less flattened laterally by mutual contact. Growth takes place more rapidly in a radial direction, and a little later by reason of lateral pressure they become almost triangular in cross-section. At the two angles of each anther on the periphery a group of cells retain their meristematic character while the rest become more vacuolated and react less strongly to stains.

In the two outer angles of each anther a layer of cells contiguous to the epidermis divides by periclinal walls, thus giving rise to the primary sporogenous and primary parietal cells. Both of these again undergo divisions. The parietal series gives rise to four layers of cells, so that the external wall of the anther early comes to consist of five layers of cells including the epidermis. In this region of the anther the greater number of sporogenous cells divide repeatedly so that an almost cylindrical mass of spore-mother-cells is developed in each angle of the anther.

As usual, the layer of sterile cells adjoining the sporogenous tissue is developed as a tapetum and presents the usual appearance of such a tissue. The cells of this layer have two or more nuclei each, and the size and chromatic content of these nuclei, as well as their deeply staining cytoplasm, mark them off in sharp contrast from the adjoining sterile tissue. The tapetal cells retain their appearance of activity almost to the time of maturity of the pollen.

The usual process takes place in the formation of microspores. These are enclosed for some time in a somewhat gelatinous envelope before they round off and develop the thick exine. The division of the nucleus of the spore takes place quite late if at all. Although almost mature anthers were sectioned, no case was found in which a microspore contained more than one nucleus.

In *Micrampelis* several cells immediately below the epidermis

divide by periclinal walls. These cells are distributed along the ridges which later plainly mark off the positions of the locules. The series thus formed gives rise to three layers of cells, one of which forms the tapetum. Outside of the tapetum only three layers of cells including the epidermis are to be found in the mature anther.

The primary sporogenous cells enter directly upon a period of growth, becoming spore-mother-cells without divisions. The mother-cells form a linear series, sometimes broadening into a narrow plate but never dividing to form a cylindrical mass as in the case of *Fevillea*. These cells become large and prominent and each gives rise to four microspores. Here as in the preceding case the nucleus of the microspore does not divide to form vegetative and generative nucleus until quite late.

In *Cyclanthera* when the rudiment of the androecium has begun to assume the form of a disk the hypodermal cells prepare for periclinal divisions in two zones, one above the other. The cells in the two narrow bands thus situated divide as in the previous types to form the primary parietal and primary sporogenous cells (FIGURE 11). The former divide again to three layers, which with the epidermis constitute the outer wall of the locule (FIGURE 12). The primary sporogenous cells do not divide to increase the number of spore-mother-cells, but merely enter upon a period of growth until the time arrives for the formation of the macrospores. Four microspores are formed from each spore-mother-cell in the usual order. They remain for some time in a pyramidal arrangement surrounded by a transparent, seemingly gelatinous envelope, and during this time the exine begins to thicken and the nucleus assumes a less chromatic aspect. As they separate the microspores become rounded off and begin to develop their characteristic markings. Almost mature pollen-grains were observed in the sections, but each contained only one nucleus. The tapetum retains its active appearance until the spores are almost mature.

But the chief interest in pollen-formation in these forms is not in the facts just cited, but in the details of the process as they appear in the division of the mother-cells. In the few members of the *Cucurbitaceae* here under consideration, the course of develop-

ment leading up to the formation of the pollen differs in no important particular. Some apparently minor differences have been noted which will be mentioned. The history of the microspores has been most carefully followed in *Micrampelis*, which is a favorable object for such a study. The principal stages in the formation of the microspore have also been noted in *Fevillea*, *Melothria*, *Cucurbita moschata*, *C. Pepo*, and *Cyclanthera*.

So far as the writer is aware no examination has been made of the cytology of the pollen-mother-cells of any of the *Cucurbitaceae*, though certain features of the vegetative cells have been studied by Zacharias.[27]

Though less favorable in some respects than some other subjects for such studies, certain features have been observed which seem worthy of attention.

The history of the microspore from this point of view begins with the formation of the primary sporogenous cell. At the conclusion of the mitosis which forms it, the sporogenous cell is not distinctly different in appearance from any of its hypodermal neighbors. A considerable number of those in its immediate vicinity have a decidedly meristematic character. At this time the cytoplasm of these cells is relatively thin as compared with the later states. The mitotic figure which is concerned in the first division of the hypodermal cell is a multipolar one, at least in the metaphase, and its chromatin is massed together in a compact zone at the equator.

The primary sporogenous cells become directly the pollen-mother-cells. They enter upon the growth period immediately after their formation, and soon become very conspicuous by reason of their size and structure. The expansion of their nuclei is the first distinctive feature shown in their growth, and this without any apparent increase in chromatic substance makes the nuclei appear quite clear, except for the single large nucleolus and their chromatin network. In appearance the cytoplasm consists of a very fine network of granular threads. The granules stain darkly and the cytoplasmic body has a grayish cast with the haematoxylon stain. At this time there is no perceptible arrangement of the cytoplasmic substance and it is equally dense in all parts. With the growth of the cell the granules increase in size slightly up to

the time of the division. At about the time of synapsis the cytoplasm undergoes an interesting change. At this time the position of the nucleus in the cell is more or less eccentric and the nucleolus and the chromatin mass are usually on the side of the nucleus nearest the cell-wall. The cytoplasm, which up to this time has shown no special differentiation, now displays a number of fine fibers running tangent to the nucleus along the arc lying opposite the chromatin mass. These fibers may be traced distinctly to the periphery of the cytoplasm, where they appear to connect with the plasmatic membrane. The cell at this time presents an appearance much as if the nucleus by rapid expansion had placed under tension some of the fibers of the cytoplasmic reticulum (FIGURE 24). Toward the periphery of the cell an apparent branching of the fibers was often noticed and frequently thicker portions which stained darkly were plainly seen. If there is any significance in these fibers it is not apparent. As the nucleus resumes its position at the center of the cell at the close of the synapsis period they are no longer visible but the meshes of the cytoplasmic reticulum appear drawn out in a radial direction from the nucleus, which is a characteristic condition just preceding the prophase. There is, however, no indication of fibers such as appear in *Cobaea*,[13] *Larix*,[1] or *Equisetum*.[20] As these changes take place there is a drawing away of the ectoplasm or "*Hautschicht*" from the cell-wall, so that the mother-cells, instead of remaining angular, become practically spherical. Cannon[3] noted the same phenomenon in the spore-mother-cells of cotton and regarded it as the normal and regular process in those cells. The same conclusion seems to be justified here by the evidence at hand and by the subsequent history of the cells arising from the ensuing divisions. The spherical form is probably an advantage in the exact division of the cells into tetrads after the manner in which they usually occur. The nucleus, which in the earlier stages shows a perfectly even curvature of its membrane, now begins to contract and its outlines are less regular. This irregularity becomes more and more pronounced until the membrane is finally dissolved in the prophase of the first division.

In FIGURE 23 are represented certain cytoplasmic bodies whose history we have made an effort to follow. At a certain stage in

the development of the mother-cells they are quite conspicuous even under a relatively low magnification (75 diameters). They are a series of short, crooked, darkly-staining fibers, which lie approximately parallel to one another on one side of the nucleus and about half way from the nucleus to the wall. They make their first appearance when the mother-cells are about half or two thirds grown and persist until the cytoplasm assumes the radial structure. As this change takes place they gradually disappear. About the time that the dark bodies disappear certain minute darkly-staining granules may be seen scattered promiscuously through the cytoplasm in its radial stage and during mitosis.

The rod-like bodies are remarkably constant features in *Micrampelis*, and appear when different staining reagents are used. It was first thought that they were portions of the nuclear chromatin which had been struck out into the cytoplasm in the process of cutting, but when it is observed that in the same section where many pollen-mother-cells are visible these bodies lie on all sides of the nuclei, such a conclusion as to their origin must be abandoned. Moreover in the same section some cells show them disposed horizontally, others show them in transverse section as a group of small black dots. It has been said that the fibers lie about parallel but occasionally they may assume a more or less radial arrangement around a certain point in the cytoplasm. They remain quite distinct up to the time when the cytoplasm begins to draw away from the cell-wall. The ends of these rods seem to weave in with the cytoplasmic meshes, especially toward the periphery of the cell where the reticulum is coarser. During the progress of the tetrad divisions the spherical, darkly-staining masses may be seen scattered through the cytoplasm, but near the close of the division they become clustered about the nuclei, and thus are divided among the microspores. They increase in size with the development of the spores and become very conspicuous until the pollen-grains near maturity when they gradually disappear. Bodies of an apparently similar nature have been found by Strasburger[24] in the pollen-mother-cells of *Larix*, and Allen[1], working upon the same subject, refers them to the class of extranuclear nucleoli and believes them to be proteid matters precipitated by fixing agents. But he finds them also in

liquid surrounding the pollen-mother-cells, where they seem never to occur in *Micrampelis*.

The history of these bodies in *Micrampelis* is against such an interpretation, inasmuch as it would be difficult to account for their collection in the form described in a circumscribed portion of the cytoplasm. Moreover the change of form which they undergo seems to indicate that they are something more than mere passive by-products. Strasburger maintains that the cytoplasmic nucleoli bear an intimate relation to the kinoplasm, and supports his contention by citing the behavior of such bodies in *Larix* and other plants, in which they appear in connection with the spindle and other parts of the spindle-fibers and disappear at the conclusion of the division. He believes, however, that they are derived from the nucleolus, inasmuch as they appear as the nucleolus disappears and vanish again with its reappearance in the daughter-nucleus.

In this view Mottier [18] concurs, and chiefly on the basis of their staining reaction states that "there is no doubt that these bodies represent nucleolar substance." He suggests furthermore that the presence or absence of extranuclear nucleoli may depend upon the activity or condition of the cell, in view of the fact that they may be present in or absent from cells of the same tissue in the same stage of development. That the bodies here under consideration in *Micrampelis* are of the same nature as those described by Mottier in *Lilium* is difficult to say, though it seems a fair assumption that they are.

In *Micrampelis* no relation between these bodies and the nucleolus could be established. They appear in the cytoplasm long before the disappearance of the nucleolus and the nuclear membrane (FIGURE 24). That nucleolar material in solution might diffuse out through the nuclear membrane and be precipitated again in the cytoplasm is possible, but it seems highly improbable, and if so it might reasonably be expected to diffuse equally in all directions. In *Micrampelis*, however, the appearance of the darkly-staining granules is at first in a particular part of the cytoplasm and that the region occupied by the fibers above referred to. These cytoplasmic fibers seem similar to those observed by Duggar [8] in *Symplocarpus* and by Lloyd [14] in *Crucianella*. In

neither of these works, however, does it appear that they bear any relation to the extranuclear nucleoli. Duggar refers to the almost simultaneous appearance of the fibers and darkly-staining granules, and regards both as due to the nuclear changes in synapsis. Lloyd regards the appearance of such cytoplasmic fibers as possibly due to the streaming of hyaloplasm or kinoplasm, from the fact of their similarity in appearance to features described by Wilson [26] and others working upon other material. That such a kinoplasmic streaming toward the nucleus occurs in *Micrampelis* is strongly suggested by the marked radial elongation of the cytoplasmic meshes during the prophase of the first division (FIGURE 25), but this feature is uniform throughout the cell.

A careful study of the material at hand has convinced the writer that in this case the extranuclear nucleoli arise from the conspicuous cytoplasmic fibers which make their appearance during the growth of the pollen-mother-cells. These fibers, at first thin and delicate, become thicker and stain more darkly, sometimes appearing as a series of nodules strung together, and again as thick crooked masses. As their development proceeds the fibers disappear and the round cytoplasmic nucleoli multiply and for a time appear in the area occupied by the fibers (FIGURES 23–68). It is recognized, however, that the phenomena observed may be open to more than one interpretation. The fibers observed lie in the center of the largest amount of cytoplasm in the cell and they must be taken as evidence of a cytoplasmic activity of some sort. It is possible that, these being the centers of special activity, they are the points at which the disposition of certain cytoplasmic products first takes place.

If we are to regard the spherical bodies in the cytoplasm of the spore-mother-cells of *Micrampelis* as extranuclear nucleoli, according to Strasburger's view, we must account for their persistence in the cytoplasm through all stages from one generation of cells to another. It does, nevertheless, seem that they are associated with the kinoplasm, inasmuch as they appear in the rod-like form to be a part of the cytoplasmic reticulum. That they are actually connected with the spindle at any stage of its development could not be determined accurately, though their position would often favor such a view. During the metaphase certain fibers may be seen

straying out into the cytoplasm from the poles of the spindle, and seem to be in contact with the dark bodies scattered through it, and when at the conclusion of the division the contracting mantle-fibers have drawn the chromosomes to the poles and the daughter-nuclei have organized, the wandering fibers have also disappeared and the dark bodies have assembled about the nuclei. Hither, however, they may have been carried passively, as there is a congestion of the granular cytoplasm about the daughter-nuclei, leaving a comparatively clear broad zone across the equator of the spindle through which the division of the cytoplasm ultimately takes place.

With the organization of the tetrads the cytoplasm undergoes a change and instead of appearing fibrillar it begins to assume an alveolar aspect. It is during this stage that the activity of the cell is directed mainly toward the differentiation of the spore and the storage of a food reserve, which would, of course, account for the predominance of trophoplasm and the relatively slight quantity of kinoplasm present. As the spore enlarges the cytoplasm is distributed about its wall and only as it nears maturity does the central vacuole entirely disappear. The spore then becomes filled with granular proteinaceous matter. The differentiation of the exine begins while the tetrads are still clinging together, and is first evident by a thickening at the points where the germinal pores are afterwards to appear. In the mature spores, as usual, these are the thinnest places in the exine. The dark cytoplasmic bodies usually become segregated into some part of the spore as it approaches maturity and the cytoplasm in their vicinity usually stains more darkly than elsewhere.

Great interest centers in the behavior of the kinoplasm during the process of cell-division, and Strasburger[24] has given careful consideration to the various expressions of its activity, showing that it is concerned not only with the development of the spindle but also with the formation of plasmatic membranes. The predominance of kinoplasm over trophoplasm is one of the most conspicuous features of the spore-mother-cells of plants, and this may appear in a variety of ways. In certain cases a distinct perinuclear zone appears just before the first division and stains very darkly, and from the fibers of this zone and the linin of the nucleus the spindle is formed, as in *Cobaea*[13], *Lavatera*[2], *Cassia*[12], *Gossypium*[3],

and other plants. On the other hand, the pollen-mother-cells of *Equisetum*[20], *Larix*[1], *Lilium*[17], and *Pisum*[4] show an entirely different condition of the cytoplasm in this respect. In these types the perinuclear zone does not exist and the origin of the achromatic figure is not so restricted. In several forms distinct fibers could be seen radiating from the nucleus toward the periphery of the cell and these fibers by folding over form a felted layer from which a multipolar spindle is later differentiated, and finally the multipolar spindle becomes bipolar by the fusion of the several poles into two. Allen[1] even suggests that this is a general process occurring in all spermatophytes. While this generalization seems not to be well founded, it does appear that we may generally refer the divisions of the spore-mother-cells in the higher plants to one type or the other. It has already been suggested (Cannon[4]) that the perinuclear zone may inhibit the formation of the spindle in the peripheral cytoplasm as it occurs in *Pisum*.

The process of mitosis as it occurs in *Micrampelis* presents some features which distinguish it from most cases. It has been pointed out above that the cytoplasm assumes a radial structure as the time approaches for the first division of the spore-mother-cell. At the same time the separation of the plasmatic membrane from the cell-wall enables the cell to assume a spherical form. The contraction of the cytoplasm is accompanied by the contraction of the nucleus so that the latter becomes angular and exceedingly distorted. Up to this time no special differentiation of the cytoplasm can be detected, but soon a few fibers can be seen running more or less parallel with the nuclear membrane; here they form a very thin reticular layer. While this change is taking place in the cytoplasm the nuclear structures are also changing. The chromatin is collecting into chromosomes and the linin appears as an almost colorless network of fine fibers which run in all directions. At this time the cytoplasm adjoining the nucleus stains a little more darkly than the rest, and as the nuclear wall dissolves, pencils of fine fibers may be seen pushing out from the nucleus into the surrounding cytoplasm. These bundles of fibers originate from the reticulum adjoining the nucleus. Soon the fibers are seen traversing the nuclear vacuole, which rapidly disappears and several poles project out from the nuclear position.

The linin fibers can no longer be distinguished as such, having been merged with those from the cytoplasm. The spindle now becomes bipolar, and the interpolar fibers are brought out in sharp contrast to the others by their stronger absorption of the stain.

Three kinds of fibers were visible: the mantle-fibers which run out from the poles of the spindle into the cytoplasm toward the equatorial region; the fibers which attach to the chromosomes and appear to draw them to the poles; and the interpolar fibers which occupy the center of the spindle and are easily distinguished throughout the anaphase and telophase. All of these except the contractile fibers are of a more or less sinuous form. The interpolar fibers are considerably thicker in their middle region, and such parts are colored quite darkly by the haematoxylon stain. During the first division the poles of the spindle do not seem to reach the peripheral cytoplasmic membrane but terminate at some distance from it (FIGURE 28). Outside of the space occupied by the spindle itself the cytoplasm is of a densely granular character, but even in relatively thin sections (3 μ) no extensions of the spindle to the "*Hautschicht*" could be seen.

The conception of an anchorage for the spindle by kinoplasmic fibers extending to the outer membrane, as expressed by Strasburger,[24] seems here hardly to be justified. It seems apparent, however, that the mantle-fibers may fix the spindle in its position by a connection with the cytoplasmic reticulum. The necessity for the fixation of the poles of the spindle in the *Hautschicht*, in order to facilitate the drawing apart of the chromosomes by contraction of the fibers, is not quite apparent. It is suggested that the interpolar fibers may act as a sort of stay, which, with a certain degree of rigidity, would facilitate the separation of the chromosomes by the contraction of the overlying fibers. The evidence at hand as to the character of the interpolar fibers certainly favors such a view.

The spindle of the second division originates like that of the first and is also multipolar in its early stages. The fibers of the cytoplasmic kinoplasm traverse the nuclear vacuole and soon obliterate it. No evidence could be found at any time of a reticulum next the nuclear wall. The spindle forms from the kinoplasmic fibers which grow in from the cytoplasm. The spindle-

fibers from the first division frequently persist through the second and after the grand-daughter nuclei are formed they may be seen connected by fibers of both preceding mitoses. The spindles of the second mitosis lie in parallel planes usually at right angles to each other but often parallel. Thus the tetrads usually appear in the ordinary pyramidal arrangement but sometimes they are all in one plane. The division of the cytoplasm takes place by constriction, a narrow groove marking off the line of division. This groove deepens until the spores are fully separated.

The nuclear contents of the cells under consideration have been difficult objects for study on account of the minute size of the chromosomes. The nucleoli are often large and conspicuous and at certain stages are apparently vacuolated. In the period of development just succeeding the cutting off of the tapetal cell, the primary sporogenous cell is distinguished from its neighbors by its dense and darkly-staining cytoplasm. The nuclei of the primary tapetal and primary sporogenous cells are at first to all appearance similar. In both the chromatin is arranged about the nuclear wall in irregular masses so that the nuclear vacuole at first appears to contain only a large nucleolus. In this case, in which the spore-mother-cell is derived directed from the primary sporogenous cell, the period of growth is begun at once and the nuclear changes keep pace with the development of cytoplasmic structures. The linin of the nucleus soon becomes more apparent and its fibers may be seen passing in different directions through the nuclear vacuole. The chromatin soon shows a tendency to cling less closely to the nuclear wall and it may be seen strung along the linin network in small irregular masses. A marked increase in the quantity of chromatin is characteristic of this stage and the lines of the nuclear reticulum are thickly beaded with chromatin granules.

The reticulum now resolves itself into a continuous thread which gradually becomes more uniform. While this change is taking place all the chromatin with the nucleolus becomes crowded into one side of the nuclear vacuole and synapsis results. Often the chromatin in synapsis may be seen as a much coiled thread with many sharp convolutions, sometimes extending almost across the nucleus. During this process the nucleolus remains undiminished in size and staining properties.

At the conclusion of the synapsis period the chromatin appears in thread-like form. The longitudinal cleavage of the thread is quite plain before its transverse divisions are apparent. A considerable shrinkage of the chromatin now takes place and at the time just before the differentiation of the spindle, it has contracted to sixteen irregular masses which in some instances appear quadruple; these portions representing the division of the chromatin giving rise to the chromosomes are very small and irregular in form. The chromosomes of *Micrampelis*, by numerous counts, number sixteen in the pollen-mother-cell.

In the earlier, presynaptic condition of the chromatin an interesting condition was observed. Instead of forming a single thread, a condition such as appears in FIGURE 33 is often apparent. The thread appears to be doubled and the chromatin-masses occur frequently in pairs. Overton [21] has described the same features in *Thalictrum purpurascens*, and Cardiff [5] finds it the regular condition in *Acer platanoides* and several other plants. In *Thalictrum* the number of the chromatin-masses agrees with the number of somatic chromosomes and the inference is that these presynaptic masses of chromatin which enter synapsis in pairs are the chromosomes of the original mother-cells (archesporium). In *Micrampelis* the double thread in a presynaptic condition is not always easily demonstrated, but in certain cases appears distinctly. The chromatin soon becomes massed around the nucleolus and synapsis results. In this condition the identity of the nuclear structures is entirely obscured, the chromatin forming a dense, darkly staining mass. It is difficult to believe that this appearance in preparations of beautifully fixed material is purely an artifact, and the opinion is gaining ground that the condition of synapsis represents the final fusion of hitherto only associated elements of different parentage, a view which agrees with other facts commonly observed during the division of the spore-mother-cell. Synapsis in the material here under consideration differs in no essential from the condition usually described, so far as could be determined. At the close of the period of synapsis the chromatin emerges in the form of a much coiled thread which shows a distinct longitudinal division (FIGURE 37). A transverse segmentation is soon apparent (FIGURES 39, 40, 41), and the chromosomes thus formed contract into short,

thick, and irregular masses (FIGURE 42). As this change is taking place the nuclear wall is becoming irregular and the incipient stages of spindle-formation appear in the cytoplasm. The evidence of true tetrad formation is not very abundant at this point, but in certain cases a double division of the chromosomes appeared to be quite clear (FIGURES 43, 44). The chromosomes at this stage become so nearly isodiametrical that it becomes practically impossible to distinguish between a longitudinal and a transverse division of the chromosome.

The first division is clearly of heterotypic form. The chromosomes appear united in the form of rings in the metaphase of the division (FIGURES 46, 47). The spindle fibers are attached to opposite sides of the ring and the separation takes place midway between the points of attachment of the spindle-fibers. The relation of the chromosomes to the fibers appears in FIGURE 50. After the separation of the chromosomes in the early anaphase of the division they round off into almost spherical bodies to which are attached certain bundles of spindle-fibers. In a transverse section of the spindle these can readily be seen and correspond in number to the chromosomes. The chromosomes during the anaphase can be readily counted and number sixteen (FIGURES 51, 52), a number found by Strasburger[23] and Guignard[11] in certain orchids. Owing to their minute size and the compact condition of the mitotic figure in the vegetative cells the number of chromosomes could not be determined, but it appears to be easily more than sixteen.

As the chromosomes draw closer together toward the apex of the spindle they become crowded together and lose their identity, so that as the daughter-nuclei are organized in the telophase they can no longer be distinguished from one another. They present the appearance of having become fused into a spireme (FIGURES 53, 54), which finally resolves itself into a reticulum, with a tendency toward pairing of the most conspicuous chromatin masses (FIGURE 55). This appearance is only transient, however, as the nucleus passes quickly into the prophase of the second division, when the chromatin appears in dense masses, at first angular and connected with many radiating fibers (FIGURE 56), later rounded off and peripherally disposed in the nuclear vacuole (FIGURES 57, 58).

The second division shows a thick mass of chromatin on a

narrow spindle. The chromosomes here diverge in the anaphase and migrate to the poles of the spindle as two compact masses in which the form and relations of the chromosomes are entirely obscured. Only in the late telophase do the chromosomes separate from one another and distribute themselves in the newly formed nuclei (FIGURE 63). The chromatin masses soon became distributed along the threads of the nuclear reticulum (FIGURE 64), which becomes much more open and enlarged with the development of the spore.

Most of the material used in this study was fixed in an acetic acid-alcohol mixture, consisting of one part glacial acetic acid and two parts 70 per cent. alcohol, which in most cases gave excellent results. The material was preserved in 85 per cent. alcohol, cleared in xylol, and embedded in paraffine. Other methods were also used, particularly in the study of *Micrampelis*, where the peculiar cytoplasmic conditions suggested the advisability of trying different reagents. In this case accordingly three methods of fixation were used viz., acetic-alcohol, sublimate acetic mixture, and the weaker Flemming solution. The stains employed were Haidenhain's iron haematoxylon, sections counterstained with Bismarck brown, Flemming's safranin-gentian-violet-orange, also cyanin-erythrosin and fuchsin-iodin-green combinations. Particular attention was given to the rod-like bodies in the cytoplasm of *Micrampelis* and the different stains were tried on the material of each fixation. In order that conditions might be otherwise the same, certain clusters of flowers of various stages of development were embedded and sectioned, forming several series of ten to fifteen slides, which were numbered in their proper sequence, and different stains applied to slides of alternate numbers in the series. In the material fixed with acetic-alcohol the rod-like bodies appeared when the preparations were stained with iron-haematoxylon or with safranin-violet-orange. When fixed with sublimate-acetic (1 per cent. acetic) mixture the same cytoplasmic structures appeared as in the preceding case, if stained with iron-haematoxylon, safranin-violet-orange or cyanin-erythrosin combinations. In material fixed with Flemming's solution they were found only when stained with the safranin-gentian-violet and orange G. The sections were cut from 2μ to 6μ in thickness.

When by such manipulations the pollen-mother-cells of the same anthers were treated with different stains as well as those of different anthers and different fixation, the chances that the unusual structures observed in the cytoplasm are due to the reagents is minimized.

SUMMARY AND CONCLUSIONS

1. The development of the pollen was followed in several forms. In each case the layer of cells immediately below the epidermis in each anther lobe divides by a periclinal wall to form primary tapetal and primary sporogenous cells. The former again divide to form two or three layers in the wall of the pollen-sac, the latter undergo repeated divisions in the case of *Fevillea* to form a mass of pollen-mother-cells, but in *Melothria*, *Micrampelis* and *Cyclanthera* no such divisions were observed. In these features the development of the sporogenous tissue and the pollen is essentially the same as described for other members of the *Cucurbitaceae* by Mirbel, Warming and others, and is in accord with the condition found in most of the seed plants.

2. The division of pollen-mother-cells was given special attention in *Micrampelis*. The principal feature of interest here is the presence of certain darkly-staining, rod-like bodies in the cytoplasm. These appear before the mother-cells have reached their full size and persist for some time, gradually breaking up as the cell prepares for its first mitosis and appearing to resolve themselves into many minute granules which stain darkly. These granules become more conspicuous between the first and second mitoses and gradually disappear as the spore approaches maturity. No evidence was gathered as to their function, though they seem to be of kinoplasmic origin. In this they are extranuclear in origin and are not derived from the nucleolus as has been observed in the case of *Larix* and some other forms.

3. The cytoplasm appears to be distinctly fibrillar. In certain cases the fibers of the reticulum are apparently stretched in lines tangential to the nucleus during the period of its rapid expansion. As the time of the first division approaches the cytoplasm presents the aspect of fibers radiating from the nucleus. The fibrillar aspect disappears with the formation of the spindle.

4. The spindle originates partly from the linin of the nuclear reticulum but mostly from the thin weft of fibers which appears about the nucleus as its wall is gradually dissolved. As the form of the nucleus changes from spherical to angular the spindle-fibers are collected into numerous pencils pointing different directions. These gradually collect to form a bipolar spindle which stands in the center of the large mother-cell and has no apparent connection with the plasmatic membrane. The form of the spindle is narrow and sharply pointed, some of its fibers spreading far out into the cytoplasm.

5. The chromatin in early stages in the development of the spore-mother-cell is inconspicuous, but as the time for division approaches it becomes distributed in paired masses through the nuclear reticulum. The masses are regarded as representing chromosomes. They finally become merged into a compact mass as synapsis approaches.

6. Synapsis here seems to be a normal phenomenon in the life of the cell. The chromatin becomes massed about the nucleolus at one side of the nuclear vacuole. From this condition it merges from a coiled thread split longitudinally, which soon segments into sixteen double pieces. These pieces become compactly massed at the equator of the spindle, contracting into rounded masses. The separation of the chromosomes is according to the heterotypic form of mitosis. The reduced number of the chromosomes is sixteen.

7. In the telophase of the first division the chromatin forms a thread which is gradually dissolved into small granules and masses almost as in the resting nucleus. The second mitosis is inaugurated by the reassembling of this chromatin into irregular masses, which become more evenly rounded and divided into two in the ensuing metaphase. Owing to the size and rounded form of the chromosomes, the characters of a homotypic mitosis were not discernible, but the appearance of the figure is essentially different from that of the first mitosis. In the telophase of the second division the chromatin distributes itself in the form of a beaded network which persists long into the development of the spore.

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LITERATURE

1. **Allen, C. E.** The early stages of spindle formation in the pollen-mother-cells of *Larix*. Ann. Bot. **17**: 281–312. *pl. 14, 15*. 1903.
2. **Byxbee, E. S.** The development of the pollen-mother-cells of *Lavatera*. Proc. Calif. Acad. Sci. III. **2**: 63–82. *pl. 10–12*. 1900.
3. **Cannon, W. A.** Studies in plant hybrids: spermatogenesis of hybrid cotton. Bull. Torrey Club **30**: 133–172. *pl. 7, 8*. 1903.
4. —— Studies in plant hybrids: spermatogenesis of hybrid peas. Bull. Torrey Club **30**: 519–543. *pl. 17–19*. 1903.
5. **Cardiff, I. D.** A study of synapsis and reduction. Bull. Torrey Club **33**: 271–306. *pl. 12–15*. 1906.
6. **Coulter, J. M. & Chamberlain, C. J.** Morphology of angiosperms. New York, 1903.
7. **Davis, B. M.** Studies on the plant cell. Am. Nat. **38**: 367–395; 431–469; 571–594; 725–760; **39**: 217–268; *f. 1–18*. (Parts I–IV, 1904. Part V, 1905.)
8. **Duggar, B. M.** Studies in the development of the pollen grains in *Symplocarpus foetidus* and *Peltandra undulata*. Bot. Gaz. **29**: 81–98. *pl. 1, 2*. 1900.
9. **Gager, C. S.** The development of the pollinium and sperm-cells in *Asclepias Cornuti* Decaisne. Ann. Bot. **16**: 123–148. *pl. 7*. 1902.
10. **Galinski, S. J.** Ein Beitrag zur Entwickelungsgeschichte des Androeceums und des Gynaeceums der Gräser. Bot. Centralb. **55**: 1–17; 62–72; 129–135; *pl. 1–3*. 1893.
11. **Guignard, L.** Nouvelles études sur la fécondation. Ann. Sci. Nat. Bot. VII. **14**: 163–296. *pl. 9–18*. 1891.
12. **Hus, H. T. A.** Spindle formation in the pollen-mother-cells of *Cassia tomentosa* L. Proc. Calif. Acad. Sci. III. **2**: 329–354. *pl. 30–32*. 1904.
13. **Lawson, A. A.** Some observations on the development of the karyokinetic spindle in the pollen-mother-cells of *Cobaea scandens* Cov. Proc. Calif. Acad. Sci. II. **1**: 168–188. *pl. 33–36*. 1898.
14. **Lloyd, F. E.** The comparative embryology of the *Rubiaceae*. Mem. Torrey Club **8**: 1–112. *pl. 1–15*. (Part I, 1899. Part II, 1902.)
15. **Merrell, W. D.** A contribution to the life history of *Silphium*. Bot. Gaz. **29**: 99–133. 1900.

16. **Mirbel, C. F. B.** Complément des observations sur le *Marchantia polymorpha*. Mém. Inst. France **13**: 39–74. *pl. 8–10*. 1835.

17. **Mottier, D. M.** Beiträge zur Kenntniss der Kerntheilung in den Pollenmutterzellen einiger Dikotylen und Monocotylen. Jahrb. Wiss. Bot. **30**: 169–204. *pl. 3–5*. 1897.

18. —— Fecundation in plants. Publication No. 15, Carnegie Institution of Washington. 1904.

19. **Naegeli, K.** Zur Entwickelungsgeschichte des Pollens bei den Phanerogamen. Zurich, 1842.

20. **Osterhout, W. J. V.** Über Entstehung der karyokinetische Spindel bei *Equisetum*. Jahrb. Wiss. Bot. **30**: 159–168. *pl. 1, 2*. 1897.

21. **Overton, J. B.** Über Reduktionsteilung in den Pollenmutterzellen einiger Dikotylen. Jahrb. Wiss. Bot. **42**: 121–153. *pl. 6, 7*. 1905.

22. **Rosenberg, O.** Über die Embryologie von *Zostera marina*. Bih. Handl. Svensk. Vetensk. Akad. **27(3)**[6]: 1–26. *pl. 1, 2*. 1901.

23. **Strasburger, E.** Über Kerntheilung und Zelltheilung im Pflanzenreich. Hist. Beitr. I. Jena, 1888.

24. —— Über Cytoplasmastructuren, Kern- und Zelltheilung. Jahrb. Wiss. Bot. **30**: 375–405. *f. 2*. 1897.

25. **Warming, E.** Untersuchungen über pollenbildene Phyllome und Kaulome. Bot. Abhandl. **2**: 1–90. *pl. 1–6*. 1873.

26. **Wilson, E. B.** Experimental studies in cytology, I. A cytological study in artificial parthenogenesis in sea-urchin eggs. Archiv. Entwickelungsmechanik der Organismen **12**: 529–596. *pl. 11–17, f. 1–12*. 1901.

27. **Zacharias, E.** Über das Verhalten des Zellkerns in wachsenden Zellen. Flora **81**: 217–266. 1895.

Explanation of plates 17–21

PLATE 17. *Micrampelis*

1. Transverse section through part of young anther showing the formation of primary tapetal and primary sporogenous cells. × 720.

2. Longitudinal section through somewhat older anther. The primary sporogenous cells have become the spore-mother-cells. × 720.

3. Transverse section through anther of still later stage. Spore-mother-cells usually in a single row in each locule of the anther. × 720.

4. Second division of spore-mother-cell. Tapetum and anther-wall. × 720.

5. Microspore, tapetum, and anther-wall. × 720.

6. Later stage of same. × 720.

7. First division of spore nucleus. × 562.

8. Division of spore nucleus completed. Generative cell near the wall. × 660.

9. Mature pollen grain. Generative cell elongated. Nucleus occupies most of the cell, and differentiation obscure. Vegetative nucleus to the right. × 660.

PLATE 18

Cyclanthera

10. Vertical section through one side of the androecium, showing division of hypodermal cell in the formation of primary tapetal and primary sporogenous cells. × 480.

11. Slightly later stage of the same. To the right are shown initial sporogenous and tapetal cells, *s* and *t* respectively. × 480.

12. Spore-mother-cells in synapsis stage. × 420.

13. Spore-mother-cells approaching first mitosis of mother-cell. × 480.

14. Mitosis of mother-cell. × 480.

15. Microspores and anther-wall. × 480.

Fevillea

16. Vertical section through anther rudiment. × 480.

17. Transverse section through young anther. Spore-mother-cells shaded; tapetum not yet differentiated. × 480.

18. Later stage of same. Tapetum, T. × 480.

19. Section through part of anther showing spore-mother-cells in synapsis. Tapetal cells strongly developed. × 480.

20 and 21. Successive stages in microspore formation. Multinucleate tapetal cells. × 480.

PLATE 19. *Micrampelis*

Mitosis of pollen-mother-cells. Figures are drawn with an Abbé camera lucida. Lens combination Zeiss 2 mm. immersion objective and compensating ocular 18. Magnification of figures 1,172 diameters.

22. Normal resting cell.

23. Appearance of rod-like cytoplasmic bodies.

24. Synapsis. Cytoplasmic fibers tangent to nucleus. Disappearance of rods and appearance of darkly staining granules.

25, 26. Contraction of nucleus and preparation for division.

27. Showing origin of spindle.

28–30. Metaphase, anaphase, and telophase of first division.

31. Mother-cell showing nuclei resulting from the first and second divisions. The section includes but three of the four nuclei.

32. Young microspore.

PLATE 20. *Micrampelis*

Plates 20 and 21 deal chiefly with the changes taking place in the nuclear structures during the first and second divisions of the pollen-mother-cells of *Micrampelis*. Magnification 2,200 diameters.

33. Relatively early condition of the nucleus in mother-cell.

34. A condition somewhat later than 33. Before synapsis.

35. Synapsis.

36. Conclusion of synapsis.

37. Slightly later than 36. Spireme emerging from synapsis and showing longitudinal cleavage.

38. Double chromosomes as seen after transverse divisions of the spireme.

39–41. Appearance of the nuclei at the stage showing transverse divisions of the spireme.

42, 43. Showing condensation of the chromosomes. It is at about this time that spindle formation begins to be apparent in the cytoplasm.

44. Appearance of some of the chromosomes taken from various nuclei at about the same stage as shown in figure 43.

45. Metaphase of first division.

48. Anaphase of first division showing form of chromosomes and relation of mantle-fibers to the same. Interpolar fibers stain darkly.

49. Section through mantle-fibers attached to chromosomes; sixteen in number.

PLATE 21. *Micrampelis*

46, 47. Metaphase of first divisions; heterotypic form.

50. Chromosomes as they appear in the metaphase of the first division attached to the fibers.

51, 52. Chromosomes as they appear in the anaphase, numbering sixteen.

53, 54. Formation of spireme in telophase of first division.

55. A condition of the nucleus reached at the conclusion of the first division.

56, 57. Prophase of second division.

58, 59. Showing persistent spindle between nuclei in prophase of second division.

60–62. Anaphases of the second division.

63. Daughter-nucleus in telophase of the second division.

64, 65. Transition from condition shown in 63 to the reticulate resting nucleus.

66–68. Showing transformation from dark cytoplasmic fibers to the extranuclear nuclei.

American ferns — VIII. A preliminary review of the North American Gleicheniaceae

LUCIEN MARCUS UNDERWOOD

The oldest known of the American representatives of this family was figured by Plumier in 1703 (*plate 28*) and this plate was taken by Linnaeus in 1753 as the type of *Pteris dichotoma* and in 1759 as the type of *Acrostichum furcatum*. After various vicissitudes this oldest species of the genus — probably because of its rarity, for it grows, apparently, only in the extinct craters of the Lesser Antilles — passed into forgotten synonymy. The first recognition of generic value in the family was made in 1793, by Sir J. E. Smith, who based the genus *Gleichenia* on *Onoclea polypodioides* of Linnaeus, an Australian species. This was followed in 1804 by Willdenow's genus *Mertensia*, based on five pectinate species, part of which were American. This generic name could not hold because of the earlier *Mertensia* Roth (1793) in the *Boraginaceae;* and this fact was noted as early as 1806, by Bernhardi, who then established the genus *Dicranopteris* in its place, basing his name on *Polypodium dichotomum* Thunb. from Japan.* It is this genus to which our American species pertain.

Robert Brown published *Platyzoma* in 1810 with a single Australian species, and in 1861 Mettenius established *Stromatopteris* with a single species from New Caledonia.† We believe that all of these represent valid genera and may be separated by the following tabulated characters:

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* DICRANOPTERIS Bernh. Neues Jour. Bot. Schrad. 1²: 38. 1806. In the face of this publication Willdenow still used *Mertensia* in 1810 as Swartz had done before him in the first *Synopsis Filicum* (1806). Raddi, Desvaux, Brackenridge, and Sturm all published under this name, and Fée continued to recognize *Mertensia* and publish species in the genus until 1869. In 1856 Hasskarl again recognized the fact that *Mertensia* for a fern genus was preoccupied and substituted the name *Mesosorus* for it.

† It is a curious coincidence that *Platyzoma*, established by an Englishman, is reduced to synonymy by recent German writers, while *Stromatopteris*, established by a German and still maintained by them, is not accepted in the *Synopsis Filicum* of Hooker & Baker.

Stems simply pinnatifid or pinnate.*	
Sori borne on the ends of ordinary veins; rootstocks creeping.	PLATYZOMA.
Sori borne on horseshoe-shaped receptacles; rootstocks erect.	STROMATOPTERIS.
Stems pseudo-dichotomous, once to many times forking.	
Sori borne on the ends of veins; segments in the form of rounded lobes.	GLEICHENIA.
Sori borne dorsally on the veins or at a fork; pinnae pectinate.	DICRANOPTERIS.

Of the above genera *Dicranopteris* is found in both the Old World and the New, extending in range from Japan to the Straits of Magellan. The other genera are confined to the southern hemisphere of the Old World. As stated above *Platyzoma* and *Stromatopteris* are monotypic, while *Gleichenia* has several species ranging from South Africa to Java and Australia.† The species of *Gleichenia* are frequent in cultivation in the conservatories of the Old World, but we have never seen any of the species of *Dicranopteris* in cultivation anywhere. The development of the sexual stage is only incompletely known, having been partially studied by Rauwenhoff,‡ but in Jamaica at least the early stages of several species are abundant on the clay banks from germinating spores to young sporophytes in all stages. The young stages of the various species could profitably be studied at the Cinchona laboratory, as all four of Diels' sections of the genus are abundantly represented within easy reach of that station.

Some of the larger members of the genus *Dicranopteris* form thickets so deep that we have seen tunnels cut through them in which men could walk erect, and once, at Tweedside, Jamaica, Mr. Maxon and the writer walked for more than half a kilometer on the bent-down branches of tangles that had overgrown an unused bridle-path, our guides, tired of cutting paths, forcibly throwing themselves upon the tangles and we following on the springing elastic masses never once touching the ground and often a meter or more above it. Nearly all the species show a pseudodichotomy, and in each fork the growing axis remains in the form of a dormant bud ready to spring up as soon as the necessities of the plant demand additional foliar expansion. The accompanying diagram

*One of the South American species of the genus *Dicranopteris* has simple pectinate stems. Too little is known of the species, however, to base any conclusions on it.

† In *Synopsis Filicum* six species of § *Eugleichenia* are recognised, but there are others.

‡ N. P. W. RAUWENHOFF: La génération sexuée des Gleicheniacées. Arch. Néerl. **24**: 157–231. *pl. 4–10.* 1890.

will illustrate the normal progress of one of the species, and it must be noted that in the main the diagram represents the plant at its simplest condition except at one point (above c') where a bud of the second order of forks is represented as producing a lateral extension of the plant, a condition possible at every one of the secondary and tertiary forks.

On account of these features some of the larger species of *Dicranopteris* do not lend themselves to what has facetiously been called "lie flat botany" since they occupy too much space in every direction to be easily reduced to the limits of the ordinary herbarium sheet, and still reveal the distinctive characters of the species. Neither "rough dry botany" nor "bottle botany" will succeed much better in transferring the distinctive characters of the larger species to the laboratory, and photography, while revealing habit in the mass, can add little to the details that go to separate technically one species from another. They must be lived with in their native haunts to impress firmly their distinctive characters. The ordinary field botanist, without knowing the necessities of the case, meets a proposition in the form of a *Dicranopteris* tangle, and simply breaks off one of the small terminal portions of possibly a fork of the second or third order with no hint of the main stem or habit of growth and brings it to some herbarium for preservation as a stumbling-block for the future. Such material unfortunately formed the basis for some of the "type specimens" of the genus and they can only be elucidated and correlated after extensive study of the plants in the field. Field-work of an intelligent character alone will ever disentangle the muddles in this genus. The *hortus siccus* will furnish some of the types but they must be interpreted by the field study in their respective type localities.

The terminology of the parts of these peculiar plants requires special notice and can best be explained by reference to the diagram (FIGURE 1). We commence with a young simple upright branch* *W*. This normally forks twice, producing a bud at x'

* This upright branch from the creeping rootstock is circinate when young and is apparently homologous with the "frond" or leaf of the ordinary fern. Like the analogous case in some of the *Lygodieae* it is utterly impractical to use such a terminology here in descriptive work. It would be particularly absurd to speak of such a tangle as we have mentioned above as "leaves" or "fronds" and yet such they appear to be morphologically.

and also at $a'a'$; at the latter points we may have pairs of pectinate pinnae simply (as shown on the right) or in some species we may have a second forking (as shown on the left), or in still other species this may be continued still further. Each species when

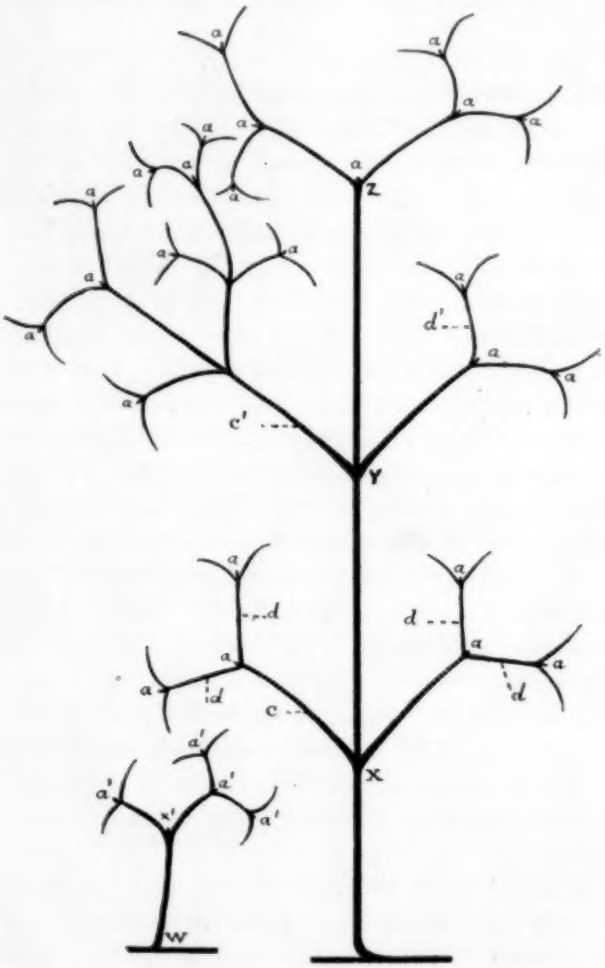

FIG. 1. Diagram of method of branching in *Dicranopteris*.

normally mature appears to have a definite limit to the number of successive forkings of the same members. So far the problem is simple, but see what happens later. At some period the bud at

x' unfolds and (*cf.* larger figure) a second fork is produced at Y which by successive forkings duplicates the simple condition first observed. The system of forks at Y may be distinguished from those below as *forks of the second order*. From Y a terminal bud may produce later a *fork of the third order* (Z) and its terminal bud may continue the process as long as the tissue of the main stem retains the power to convey nourishment. Even this condition is comparatively simple, if it would remain so, as it does in certain species; but in others, buds everywhere developed at the lateral forks as at a, a, a, a, may unroll and produce an interminable array of complications. A moderate example of this is shown at the left-hand fork above Y; from this simple example it will not be difficult to imagine the possibilities of complication arising in a vigorous upright stem. The primary branches at c, c, may be called the *primary internodes;* at d, d, d, d, we have the *secondary internodes*, and so on through the entire series of the pseudo-dichotomy.

In the field it is of prime importance to get the primary fork in a normal condition; in it the characters of the bud-scales and the extent of the decurrence of the segments on the secondary and primary internodes is of great importance. Often these are both naked except for a casual stipule-like segment at the bud itself; in others the secondary is pectinate like the upper pinnae while the primary is naked; in others still the primary is pectinate on the inner side or in some species on both sides; so far as we have been able to see, these characters are fairly constant. One species (*D. pectinata*) presents a modification of this method of forking, the alternate forks producing merely a pair of pectinate pinnae, while the opposite one produces a second fork of which the alternate internode again produces a pair of pinnae, while the other goes on as before, thus forming an apparently zigzag axis and withal most graceful sprays, as the species is vine-like and often reaches a length of several meters.

Hooker and Baker recognized twenty-one species in their *Gleichenia* § *Mertensia* * (which is *Dicranopteris*) eight of which are

* *Synopsis Filicum* ed. 2. 12, 15, and 449. 1874. Besides this two of Mettenius' species published in 1864 are included in the Index and referred to p. 449 of the text, but no mention of them occurs on that page or elsewhere in the work.

exclusively American and two others are regarded as common to the tropics of both hemispheres, while the other eleven are exclusively Old-World species ranging from Japan and Hawaii to Tasmania and South Africa. Strikingly in contrast with this treatment is the arrangement given by Sturm of the Brazilian species,* of which he describes twenty-five; almost half of which (twelve) are reduced by Hooker and Baker under the single species, *Gleichenia pubescens*, with their characteristic lack of recognition of specific characters. Sturm's treatment, although nearly a half century away from the present, is the only critical and reliable one the American species have ever received, but concerns the South American species only. The species extending into Mexico and the West Indies have never received special attention, but their treatment has usually been that of *Synopsis Filicum*, in which the species are massed under four names as follows:

1. *Gleichenia longissima* Blume. (Type from Java!)

2. *Gleichenia pubescens* H. & B. (Type from Venezuela and never examined by the authors of *Synopsis Filicum*!)

3. *Gleichenia pectinata* Presl. (Type from Caracas, Venezuela; a common tropical American species.)

4. *Gleichenia dichotoma* Willd. (Type from Japan!) †

The four categories which these tangles typify were made to stand for four sections of the genus by Diels,‡ and some of them on account of differences in spore characters, have been thought worthy of higher rank.§

1. Of the four tangles mentioned above, the first was founded on a Javan plant, and represents a large group of species, two of

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* *Flora Brasiliensis* 1[1]: 219–238. 1859.

† We have now no reason for believing that any species are common to the Old World and the New.

‡ *Die natürlichen Pflanzenfamilien* 1[4]: 353–355. 1900.

§ Spore characters, except in a few genera, have never been considered in separating ferns specifically or generically. And yet we have two very distinct types of spore that appear to be somewhat fundamentally connected with the division of the spore mother-cell. One of these is the ordinary "reniform" or diplanate type which in reality is simply a quarter of a sphere divided axially and rounded on the sharp edges; the other, producing the so-called "sphaero-tetrad" or triplanate type, is formed by a division into 4's radiating from the center of the sphere with subsequent rounding of the edges. It would be interesting to know if the gametophyte bears any relation to this diverse origin of the spore.

which are found in the American tropics and a considerable number of species are widely distributed in the Old World.* The members of this group are distinguished by forming a single fork, each branch of which develops directly into a long bipinnate portion; as in the other sections the bud at the fork may develop into forks of the second and third orders forming an indefinite growth at the end of the axis. This group forms the section *Diplopterygium* of Diels.

2. The species of the second group, which form the section *Holopterygium* of Diels, have the characteristic forking indicated in FIGURE 1, with the segments decurrent on the nodes sometimes even to the primary ones. It was in this section that Sturm characterized a dozen South American species in 1859, and a resurvey of the same area at the present time would probably double that number; this work we hope later to be able to accomplish when the types in European herbaria have been studied still further, for without this no progress is possible. Most of the West Indian and Mexican species have been confused with *Gleichenia bifida* and *G. pubescens*, both originally described from South America, but a study of type material has convinced me that neither of these species occurs in present collections north of Panama. This is strictly in accord with the conclusion reached long ago by

* Among other members of this group the following species submerged by reduction to synonymy, which we have studied at Kew and Berlin, we regard worthy of specific recognition:

Dicranopteris glauca (Thunb.).

Polypodium glaucum Thunb.; Houtt. Nat. Hist. 14:177. 1783. (Type from Japan.)

Dicranopteris glabra (Brack.).

Mertensia glabra Brack. Wilkes Expl. Exp. 16:292. 1854. (Type from Hawaii.)

Dicranopteris gigantea (Wall.).

Gleichenia gigantea Wall. Cat. n. 157. 1827 (*nomen nudum*); Hook. Sp. Fil. 1:5. *pl. 3 A*. 1844. (Type from Nepal.)

Dicranopteris longissima (Blume).

Gleichenia longissima Blume, Enum. Pl. Jav. 250. 1828. (Type from Java.)

Dicranopteris arachnoides (Hassk.).

Mertensia arachnoides Hassk. Jour. Bot. Hook. 7:322. 1855. (Type from Java.)

It is more than likely that other species of this section are confused in European herbaria, particularly with *D. gigantea* and *D. arachnoides* of the above list.

Sturm, who showed that the extension of range of *G. pubescens* at least was southward from its type locality rather than northward. Recently Dr. Christ has delimited a number of Costa Rican species, unfortunately with very poorly prepared material and probably without due reference to the species of South America. A number of his species have been re-collected in excellent specimens by Mr. Maxon, but much more field work in that prolific region will be necessary before we reach the end of our knowledge of the range of species. We have separated thirteen species in this section with three others still in the position of *species inquirendae*.

3. The section *Acropterygium* of Diels is characterized by bearing no segments on any of the internodes, the branches all terminating in a single pair of pinnae. To this section belongs *D. pectinata*, of wide distribution, one of the most graceful of the genus.*

4. The last section, *Heteropterygium* of Diels, is most peculiar of all in its branching. As in the last section there are no decurrent segments, but after the second forking and each succeeding one, a branch is deflected downwards on either side of the fork so as to make an angle of about the same degree of aperture as the fork itself. These deflected pinnae may be nearly as large as the regular pinnae of the plant or, in other species, may be reduced to a simple pinnule only slightly larger than the ordinary segments of the pinnae of the same plant. The type of this section as well as of the genus *Dicranopteris* is the plant described by Thunberg from Japan as *Polypodium dichotomum*. It is uncertain whether the Malayan plant which has a still earlier name is identical with this species or not.† In any case the American

*Commencing with Raddi, followed by Hooker (Sp. Fil. 1: 11,12. 1844), *Mertensia glaucescens* H. & B. has been reduced to synonymy with this species, without taking the trouble to examine Willdenow's type. The species proves to be a member of a distinct section (*Holopterygium*) from the present species and is to be compared with the glaucous species of that section more recently described from South America. The type locality of *M. glaucescens* is Santa Cruz, Venezuela.

†The Malayan plant has been called *Gleichenia linearis* and has the following synonymy:

Dicranopteris linearis (Burm.)

Polypodium lineare Burm. Fl. Ind. 235. *pl. 67. f. 2.* 1768. (type from Java); not *Polypodium lineare* Thunb. which belongs to a distinct family, but as a homonym will require a new name when placed in its proper genus.

Gleichenia linearis Clarke, Trans. Linn. Soc. II. 1: 428. 1880.

species, which has a relatively large range, is distinct from either the Japanese or Malayan species, and has already been twice named.

With this general account of the genus and its sections we present a preliminary synopsis of the North American species:

Primary branches bipinnate. (§ *Diplopterygium* Diels.)
- Pinnules contiguous, mostly alternate. 1. *D. Bancroftii.*
- Pinnules distant, mostly (?) opposite. 3. *D. Brunei.*

Primary branches simply pectinate or again (sometimes repeatedly) forking.
- Branches all naked up to the final pair of pectinate pinnae.
  - With a pair of reflexed pinnae at each fork. (§ *Heteropterygium* Diels.) 7. *D. flexuosa.*
  - Without reflexed pinnae at the forks. (§ *Acropterygium* Diels.)
    - Ultimate pinnae sessile. 15. *D. pectinata.*
    - Ultimate pinnae stalked (*i. e.*, the rachises naked at the base).
      - Rachises zigzag, with reflexed segments. 17. *D retroflexa.*
      - Rachises straight, with horizontal segments. 16. *D. pteridella.*
- Branches (some or all) pectinate; pinnae pinnatifid to the base. (§ *Holopterygium* Diels.)
  - Once forked, the forks of the second and successive orders appearing like a bipinnatifid leaf; sinuses between the teeth broad. 13. *D. orthoclada.*
  - Twice to four times forked.
    - Primary internode (*i. e.*, stem between 1st and 2d fork) naked.
      - Under surface more or less tomentose. 5. *D. cubensis.*
      - Under surface smooth or at most faintly pubescent; rachises mostly scaly.
        - Pinnae narrow (under 3 cm. wide); mostly 4-forked.
          - Scales of axillary buds dark-fulvous; segments granular-glaucous beneath. 4. *D. costaricensis.*
          - Scales of axillary buds pale-brown; segments faintly pubescent beneath, not glaucous. 11. *D. jamaicensis.*
        - Pinnae wider (3.5–5 cm.).
          - Under surfaces glaucescent; rachises densely-covered with pale spreading scales. 2. *D. bicolor.*
          - Under surfaces faintly pubescent; rachises with scattered scales.
            - Scales of axillary buds dark-fulvous; scales of ultimate rachises with dark centers. 12. *D. mellifera.*

Scales of axillary buds pallid; scales of ultimate rachises uniformly pale. 14. *D. palmata.*

Primary internode naked on the outside, at least below.

Pinnae narrow, 2 cm. or less wide.

Under surface thickly set with short erect reddish clavate bodies giving a granular appearance; primary internodes 2 cm. or less long. 6. *D. farinosa.*

Under surface smooth or glaucous-mealy, pale; primary internodes longer, 4–5 cm. long. 18. *D. strictissima.*

Pinnae wider, 2.5–6 cm.

Under surfaces slightly pubescent; ultimate rachises densely scaly. 9. *D. furcata.*

Under surfaces tomentose; ultimate rachises tomentose at first, becoming smooth. 8. *D. fulva.*

Primary internode (if any) fully pectinate; segments contiguous; primary axis prominent, producing (apparently) lateral branches. 10. *D. intermedia.*

LIST OF THE NORTH AMERICAN SPECIES

1. **Dicranopteris Bancroftii** (Hook.).

Gleichenia Bancroftii Hook. Sp. Fil. **1**: 5. *pl. 4 A.* 1844.

TYPE LOCALITY: Jamaica, *Bancroft.*

DISTRIBUTION: Mountains of Jamaica at altitudes of about 1200–1500 meters; also in Costa Rica, Colombia, Venezuela, Ecuador, and Bolivia.

ICON: Hooker, *loc. cit.*

This species was properly distinguished from the Old World representatives of the *longissima* group by Hooker, and this just opinion was abandoned when he cast all rational ideas of geographic distribution aside, and as well all rational conceptions of species limitations. The species is a most graceful plant in spite of its large size; it often forms sprays four or five meters long overhanging dry banks. Its allies are discussed in the footnote on page 249.

2. **Dicranopteris bicolor** (Christ).

Gleichenia bicolor Christ, Bull. Herb. Boiss. II. **6**: 279. 1906.

TYPE LOCALITY: Valle del Rio Navarro, Costa Rica, *Wercklé.*

DISTRIBUTION: Known only from the mountains of Costa Rica, alt. about 1400 meters.

This very distinct species was first collected by J. J. Cooper and was referred by Mr. Baker to the all-embracing *Gleichenia pubescens*, as "a large glabrous form." From Cooper's fragment we had recognized a plant unique and distinct from any known species as early as 1898; the material then at hand was too meager for description.

3. **Dicranopteris Brunei** (Christ).

Gleichenia Brunei Christ, Bull. Herb. Boiss. II. **5**: 13. 1905.

TYPE LOCALITY: El Desengano, Costa Rica, *Brune*.

DISTRIBUTION: Known only from its type collection. Dr. Christ has kindly favored me with a part of spray which appears to be rather close to *D. Bancroftii*.

4. **Dicranopteris costaricensis** sp. nov.

A flabellate, 3–4-forked plant with narrow pinnae. Rootstock creeping; main stalk slender, 2 mm. in diameter, smoothish or with scattered scales; primary forks diverging at an angle of 100°, the primary internodes 4–8 cm. long, with 1 or 2 small obtuse lobes at the base; terminal bud large with dark-brown, ciliate-margined scales, sometimes forming a forking of the second order; secondary branching diverging at an angle of 80°–90°, the secondary internodes 4–6 cm. long, pinnate on one or both sides in the lower half; tertiary branching at an angle of 40°–60°, the internodes 5–6 cm. long, uniformly pinnate throughout, sometimes not forming a quaternary fork; pinnae 12–20 cm. long, 1.25–2 cm. wide, the segments short, glaucous underneath, with strongly revolute margins; veins once forked; rachises more or less densely covered underneath with delicate brown ciliated scales; sporangia in 3's or 4's.

Type from Costa Rica, Volcan Poas, alt. 2600 meters, *J. Donnell Smith 6859;* Volcan de Turrialba, alt. 2800 meters, *Pittier* (*J. D. S. 7486*).

This very distinct Costa Rican species has been confused by nearly every writer with *Gleichenia revoluta* H. & B., a species described from Ecuador, which differs materially in its narrower pinnae, different vestiture of the segments, and different bud-scales and decurrence of the segments on the internodes.

5. **Dicranopteris cubensis** sp. nov.

A straggling plant of wayside banks, with stems a meter or more high. Rootstocks wide-creeping, slender; 3-forked at the

first branching, 2-forked at the second; primary internodes 3.5–4.5 cm. long, naked with more or less appressed pubescence, the buds rather large with small pallid finely ciliate scales; secondary internodes about equal length, sometimes nearly naked, but sometimes with segments decurrent from the tertiary forks one-half to two thirds the length; pinnae 25–30 cm. or more long, 5–7 cm. wide, the segments narrow, widening at the base, separated by 2–3 times their width, smooth above, covered beneath with a fine pure white appressed tomentum in which the sori are embedded; veins forked, mostly near the base, distinct; sporangia mostly in 3's and 4's.

On clay banks, slopes of El Yunque, near Baracoa, Cuba, *Underwood & Earle 1416* (type), *1196*; also collected by *Wright 921* (in part), *1810*.

6. **Dicranopteris farinosa** (Kaulf.).

Mertensia farinosa Kaulf. Wesen der Farrenkr. 37. 1827.

Mertensia subtrisperma Fée, Mém. Foug. **11**: 122. *pl. 32. f. 2.* 1866. (Type from Guadeloupe.)

TYPE LOCALITY: "Deren Vaterland ich nicht kenne" — *Kaulfuss.*

DISTRIBUTION: Known only from the island of Guadeloupe.

ILLUSTRATIONS: Kunze, Anal. Pterid. 6. *pl. 3.* 1837; Fée, *loc. cit.*

This is another characteristic species that has been strangely misunderstood in spite of the two excellent illustrations cited above, both of which call attention particularly to the very unique covering of the under side of the segments which we have seen in no other species of the family. Under the name *Gleichenia farinosa* or *Mertensia farinosa* it has been mistakenly reported from all the greater Antilles. It appears very rarely in collections and has probably a limited range on the islands of the Lesser Antilles. Although Kaulfuss was not aware of its original place of collection, his figure in Kunze's *Analecta* is unmistakable and it is more than probable that he found his specimen among some of the plants brought in by Sieber's collectors.

7. **Dicranopteris flexuosa** (Schrad.).

Mertensia flexuosa Schrad. Goett. Gel. Anz. 863. 1824.

Mertensia rigida Kunze, Linnaea **9**: 16. 1834. (Type from Chibangata, Peru, *Poeppig.*)

Gleichenia flexuosa Mett. Ann. Lug. Bat. **1**: 50. 1863.

Gleichenia rigida Bommer & Christ. Bull. Soc. Bot. Belg. **35**: 174. 1869. Not *Gleichenia rigida* J. Sm.

TYPE LOCALITY: Brazil, *Maximilian Prinz Neuwied.*

DISTRIBUTION: Lower elevations up to 800 m. alt., Porto Rico, Cuba, Jamaica, and southward from Colombia along the Andes to Peru and Brazil.

ILLUSTRATION: Mart. Icon. Crypt. Bras. *pl. 60. f. 1.*

This is the American representative of a rather complicated group of plants that have been unceremoniously massed under the name of *Gleichenia dichotoma.* This last species was described and figured from Japan by Thunberg as *Polypodium dichotomum* and may be distinct from the earlier Malayan representative of the group described by Burmann as *Polypodium lineare.* In any case the Malayan representative will bear the name *Dicranopteris linearis* (Burm.) as noted above. The fibro-vascular bundles of the last-named species are wiry and elastic and are used by the Malayans for weaving hats or hat frames and other articles. The Javan species is much larger than its low American representative and this accounts in part for the confusion which has placed several Old World species ranging from Hawaii and Japan to Java, Nepal, Madagascar and Fernando Po in one species, when there are certainly several as indicated by their mummied fragments preserved in European herbaria.

8. **Dicranopteris fulva** (Desv.).

Mertensia fulva Desv. Ann. Soc. Linn. Paris **6**: 200. 1827.

This commonest species of the island of Jamaica has been in recent years strangely confused with the *Mertensia pubescens* of Willdenow, which was originally described from South America. It was characterized in 1827 by Desvaux in the following terms which appear unmistakable:

"Stipite et rachi dichotomo glabris; frondibus pinnatis; pinnis per dichotomiam decurrentibus, pectinato-pinnatifidis: pinnulis linearibus, elongatis, subobtusis, subtus fulvo-tomentosis; sporangiis subquaternatis. Habitat in montibus ceruleis Jamaicae."

The Hookerian school, Grisebach, and Jenman all confused this species with *Mertensia pubescens,* notwithstanding the fact that Sturm as early as 1859 had definitely delimited that much smaller South American species which Willdenow himself had

described as "*subtus albido villosis*," to say nothing of numerous other characters.

The present species forms immense thickets on banks and overgrows paths that are long neglected. Its general habit may be seen from a photograph taken last year in Porto Rico by Dr.

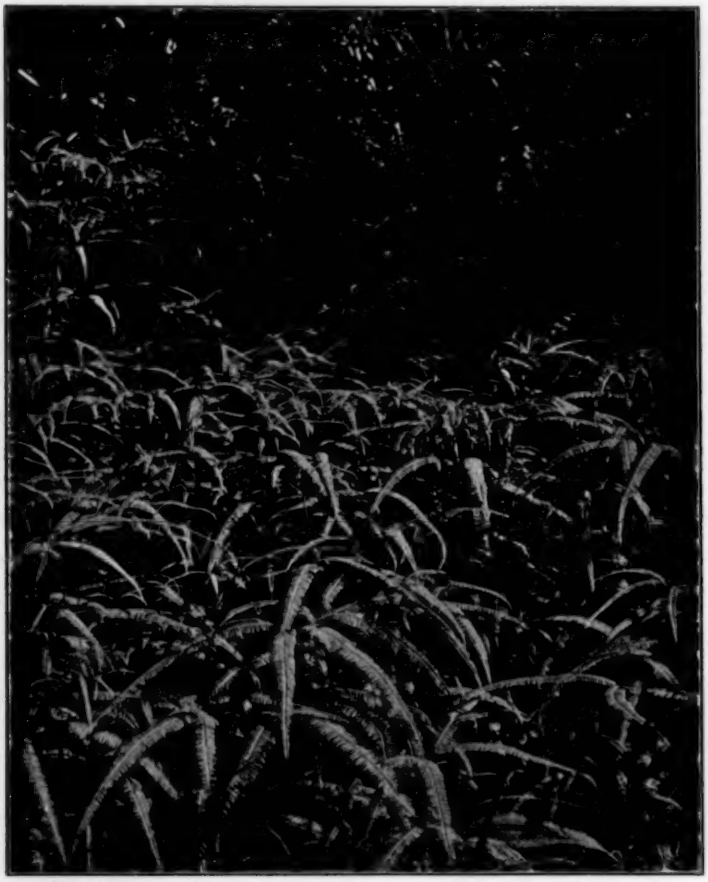

FIG. 2. Bank covered with *Dicranopteris fulva*, Porto Rico. (Courtesy of the *Journal of the New York Botanical Garden.*)

M. A. Howe which is here reproduced by the courtesy of the New York Botanical Garden (FIGURE 2). This is the species alluded to above (page 244) at the Tweedside plantation, Jamaica.

DISTRIBUTION: Cuba, Jamaica, Porto Rico, Hispaniola, and in

Mexico from Orizaba and Chiapas southward to Guatemala, Costa Rica and Panama. It is not always possible to cite specimens from the miserable fragmentary tips which even some of the recent collectors bring back to herbaria after a laborious and expensive journey to add to the knowledge of our tropical flora.

9. **Dicranopteris furcata** (L.).

Pteris dichotoma L. Sp. Pl. 1076. 1753. Not *Dicranopteris dichotoma* Bernh.

Acrostichum furcatum L. Syst. Nat. ed. 10. **2**: 1321. 1759. (Based on Plumier *pl. 28*, the same as had previously served as the type of *Pteris dichotoma*.)

Polypodium furcatum Sw. Jour. Bot. Schrad. **1800**^{2}: 28. 1801.

Gleichenia furcata Spreng. Syst. Nat. **4**: 25. 1827.

Mertensia furcata Willd. Vet. Ak. Nya Handl. 166. 1804.

Mertensia grandis Fée, Mém. Foug. **9**. 31. 1857 (nomen nudum); Mém. Foug. **11**: 120. 1866. (Type from La Soufrière, Guadeloupe.)

Rootstock unknown; upright stems stout, 5–6 mm. in diameter, covered above and when young with copious pale lanceolate scales; primary branches forming an angle of 80°, with one or two pinnae on either side at the base of the internode, which is 3 cm. long and scaly like the main stalk; occasionally forming a secondary branch with the second internode 6 cm. or more long, fully pinnate on both sides; pinnae 12–20 cm. long, 4.5–6.5 cm. wide in the middle, narrowed slightly toward each end, elliptic, the segments about 3 mm. wide, tapering mainly near the tips; under surfaces nearly smooth except the rachises which are densely scaly.

TYPE LOCALITY: Morne de la Calebasse, Martinique; based on Plumier, *pl. 28*.

DISTRIBUTION: Craters of extinct volcanoes [Martinique], Guadeloupe, and St. Kitts (Mt. Misery, *Britton & Cowell 526*).

ILLUSTRATION: Plumier, *loc. cit.*

This species has been strangely misunderstood and until the collection of fresh material by Britton and Cowell in 1900 it was impossible to correlate the species with other collections, especially of the *Mertensia grandis* Fée, which we have since seen in his collection and which was evidently based on plants with rather longer pinnae. The plants from St. Kitts exactly match the illus-

tration from Plumier. The plant has not recently been collected in Martinique and is not likely ever to be collected there again. It should be sought at the summits of the higher volcanic islands of the Lesser Antilles. In St. Kitts it goes by the name of "stag-horn fern."

By strangely following somebody's error, Christensen * refers *Mertensia grandis* to *Gleichenia Bancroftii* (*Dicranopteris Bancroftii*), a member of a distinct section of the genus.

10. **Dicranopteris intermedia** (Baker).

Gleichenia intermedia Baker, Jour. Bot. **25**: 24. 1887.

Gleichenia axialis Christ, Bull. Herb. Boiss. II. **5**: 14. 1905.

(Type from Rio Navarro, *Wercklé*.)

TYPE LOCALITY: Costa Rica, *J. J. Cooper*.

DISTRIBUTION: Costa Rica.

Dr. Christ in some way formed the impression that Baker's species was "une espèce évidemment alpine," whereas Cooper's collection was from near Cartago and not far from the type locality of *G. axialis*, which is without question a redescription of Baker's plant. It really does prevent errors to visit Kew, but it is hard to convince continental fern students of that fact.

11. **Dicranopteris jamaicensis** sp. nov.

A mountain species with narrow pinnae much forked, sometimes proliferous and forming low thickets. Rootstocks creeping, frequently branched with abundant brownish scales; stems erect, 25–60 cm. long, 2–4-forked; buds densely covered with pale-brown ciliate scales; primary internodes naked or with a very few small segments on the inner side at base, scaly at first, becoming smooth and shiny, 3–9 cm. long; secondary internodes nearly naked or more often with segments on both sides below or all the way up, densely scaly as are the rachises with narrow pale-brown ciliate scales; tertiary internodes fully pectinate; pinnae 16–22 cm. long, rarely more than 2 cm. wide, with numerous closely placed segments separated by less than their width; under surfaces smooth, veins distinct, once forked, a third above the base; sori pale, in 3's and 4's.

Blue Mountains of Jamaica, *Underwood 1511* (type), *508, 919, 2500, 2552, 3209; Maxon 2617;* also collected by *Jenman, Hart* and others.

* Index Filicum 423. 1906.

Confused by Jenman with *Gleichenia Matthewsii* Hook., a Peruvian species with a widely different vestiture throughout.

12. **Dicranopteris mellifera** (Christ).

Gleichenia mellifera Christ, Bull. Herb. Boiss. II. **6**: 28. 1906.

TYPE LOCALITY: Valle del Rio Navarro, Costa Rica, *Wercklé*.

DISTRIBUTION: Known only from Costa Rica.

13. **Dicranopteris orthoclada** (Christ).

Gleichenia orthoclada Christ, Bull. Herb. Boiss. II. **5**: 16. 1905; *ibid.* **6**: 282. 1906.

Gleichenia intermedia dissitifolia Baker, Jour. Bot. **25**: 24. 1887. (Type from Costa Rica, *J. J. Cooper.*)

TYPE LOCALITY: Costa Rica, *Wercklé 212.*

DISTRIBUTION: Known only from Costa Rica.

14. **Dicranopteris palmata** (Schaffner) sp. nov.

Mertensia palmata Schaffner; Fée, Mém. Foug. **9**: 32. 1857 (*nomen nudum*).

Gleichenia palmata Moore, Ind. Fil. 380. 1862 (*nomen nudum*).

A smoothish species with upright stems 3–4-forked, the primary and secondary internodes naked, the ultimate pinnae diverging at an angle of about 30°. Rootstock creeping, sending up strict branches (stems) 60 cm. or more high, the upper portion 4–6 mm. in diameter, smooth, olive-brown; primary branches diverging at an angle of 90°, 7–8 cm. long, naked except for a few scattering scales; secondary branches diverging at an angle of 60°, the internodes 3.5–4 cm. long, with a pair of bracts at the base and a line of linear scales along the inner side, otherwise naked; tertiary branches diverging at an angle of 30°–40°, the internodes 5–6 cm. long, pinnate on both sides throughout; quaternary and final branches forming an angle of 30°, the pinnae 20–25 cm. long, 3 cm. wide, tapering gradually to the point; segments 2.5 mm. wide, the margin often finely revolute, blunt, with a few scattered hairs beneath; sporangia in 3's or 4's; rachises pale reddish-brown with scattered ciliate scales.

Type from moist woods, Orizaba, Mexico, *Pringle 6129;* also collected by *Liebmann, Schaffner,* and *Bourgeau;* also common at 1500 m. in the Blue Mountains of Jamaica, occurring singly and not forming thickets like the allied species.

This species was first recognized by Schaffner as distinct and given a manuscript name which was published but not described

by Fée under *Mertensia* and transferred by Moore to *Gleichenia;* although the plant has thus been known for nearly fifty years it has remained undescribed. The plant was distributed by Mr. Pringle as "a smooth form" of *Gleichenia pubescens*, but has nothing to do with the species distributed by him under that name in the collection of the same year (*no. 6130*). The Jamaica plants which we are unable to distinguish from the Mexican occur at points above Morce's Gap on the trail to John Crow Peak and above Cinchona on the road to New Haven Gap. Jamaica collections in the herbarium of the New York Botanical Garden are as follows: *Clute 184, Underwood 618, 965, 1245, 2033, 2097*, and *3138*. Mr. Jenman confused this species with *Gleichenia furcata*, to which species, as properly understood, it is not closely related.

15. **Dicranopteris pectinata** (Willd.).

Mertensia pectinata Willd. Vet. Ak. Nya Handl. 168. *pl. 4.* 1804.

Gleichenia pectinata Presl, Rel. Haenk. **1**: 71. 1825.

TYPE LOCALITY: Caracas, Venezuela.

DISTRIBUTION: Generally distributed through tropical America. Specimens are at hand from Jamaica, Hispaniola, Porto Rico, Dominica, St. Vincent, Martinique, Guadeloupe, Grenada, Trinidad, Guatemala, and Panama; also from Colombia, Guiana, Ecuador, Bolivia, and Brazil.

16. **Dicranopteris pteridella** (Christ).

Gleichenia pteridella Christ, Bull. Herb. Boiss. II. **6**: 284. 1906.

TYPE LOCALITY: Costa Rica, *Wercklé.*

DISTRIBUTION: Known only from its type collection.

17. **Dicranopteris retroflexa** (Bommer).

Gleichenia retroflexa Bommer, Bull. Soc. Bot. Belg. **35**: 175. 1896.

Gleichenia intermedia flexuosa Baker, Jour. Bot. **25**: 24. 1887. (Type from Costa Rica, *J. J. Cooper*).

TYPE LOCALITY: La Palma, Costa Rica, *Pittier 1471.*

DISTRIBUTION: Known only from the mountains of Costa Rica, alt. 1800 m.

ILLUSTRATIONS: Christ, Bull. Herb. Boiss. II. **5**: 15. 1905.

This remarkable species was first described by Mr. Baker, in

1887. Having already described a new species (*Gleichenia intermedia*) from the collections of J. J. Cooper, he evidently lost courage upon finding two others in the same collection undescribed and referred them both, as varieties, to his *G. intermedia*. One of these is *D. orthoclada*, described by Dr. Christ, and the other is the present species, which is the most peculiar of all the anomalies in a strange genus. We were at first inclined to regard the scrappy material collected by Cooper as a sport, but ample material collected by Mr. Maxon places us in the possession of a sufficient illustration of the species to doubt its normality no longer.

18. **Dicranopteris strictissima** (Christ).

Gleichenia strictissima Christ, Bull. Herb. Boiss. II. **5**: 13. 1905.

Gleichenia glaucina Christ, Bull. Herb. Boiss. II. **6**: 283. 1906. (Type from Navarro, Costa Rica.)

TYPE LOCALITY: Costa Rica, *Wercklé 215*.

DISTRIBUTION: Known only from Costa Rica, alt. 1450–1550 meters.

With specimens communicated from Dr. Christ before us, we are not able to separate these two species. Wercklé's specimens, unfortunately, do not give us good representatives of the species. More recently however Mr. Maxon has gathered some beautifully preserved specimens from La Palma (*no. 432*); these are of the *glaucina* type being strikingly glaucous beneath, a character on which too much reliance should not be placed in separating the members of this genus. The original *G. strictissima* has smooth but not glaucous under surfaces, but seems to differ in no other way.

SPECIES INQUIRENDAE

MERTENSIA GLEICHENIOIDES Liebm. Mex. Bregner 144. 1849. (Type from Cuapa, Dept. Vera Cruz, Mexico, *Liebmann*.)

Gleichenia Leibmanni Moore, Ind. Fil. 379. 1862.

This species we have never seen. A tracing of a single fork appears in the collection of Mettenius at Berlin, and shows a narrow elongate pinna with crenately lobed segments wholly unique in the genus. It is only known from its type collection, and Mr. Christensen, who is at the Copenhagen museum where

Liebmann's types should be, places it among the little-known species.

GLEICHENIA TRACHYRHIZOMA Christ, Bull. Herb. Boiss. II. **6**: 280. 1906. (Type from Valle del Rio Navarro, 1,400 meters, *Wercklé*.)

GLEICHENIA BREVIPUBIS Christ, Bull. Herb. Boiss. II. **6**: 280. 1906. (Type from Valle del Rio Navarro, Costa Rica, alt. 1,400 meters, *Wercklé*.)

Although Dr. Christ has sent fragments of these two Costa Rican species we are unable to differentiate them satisfactorily in our synopsis, as they do not show distinctive characters; Wercklé's specimens are poorly preserved and do not show essential parts of the plants.

COLUMBIA UNIVERSITY.

Studies on the flora of Southern California — II.

LE ROY ABRAMS

Xylothermia montana tomentosa subsp. nov.

Distinguished from the typical form by the broader and larger leaves which, together with the twigs and legumes, are densely hoary-tomentose.

This subspecies is confined to the chaparral region of Southern California, extending from the vicinity of Los Angeles to the Mexican boundary. The typical form extends from Santa Barbara northward both in the Coast Ranges and the Sierra Nevada.

Type collected by the author (*3530*) near El Nido, San Diego County, May 20, 1903.

Chamaebatia australis sp. nov.

Chamaebatia foliosa var. *australis* Brandegee, Bot. Gaz. **27**: 447. 1899.

"Much less glandular-pubescent than the type; leaves narrower in outline, three times as long as wide and barely more than twice pinnate, calyx-lobes shorter: ovary smooth." These are characters that hold well and since no intermediate forms have been found it seems only logical that a plant so isolated geographically should be considered as a distinct species. The range and habitat of the two species, as pointed out by Brandegee, are quite different. In addition to the localities cited by Brandegee may be added San Ysidro Ranch, Lower California, *Mearns 3861*, July 2, 1894.

ADENOSTOMA FASCICULATUM DENSIFOLIUM Eastwood, Bull. Torrey Club **32**: 199. 1905

This variety was based upon specimens collected by Mr. Fordyce Grinnell Jr. on Mt. Wilson, near Pasadena. During a short stay in Southern California the past summer I had an opportunity to study somewhat closely the chamiso in the mountains

about Pasadena, and from these observations I am convinced that Grinnell's specimens were from merely abnormal stunted shrubs. The chamiso is fairly common there, and is normally quite typical *A. fasciculatum*.

Xanthoxalis californica sp. nov.

Perennial from a stout woody root, bearing many rather stout branching woody rootstocks at the crown; stems decumbent, tufted at the ends of the rootstocks, 1–3 dm. long, very sparingly and loosely villous; leaflets pale-green, villous; cyme only 1–flowered or mostly 2–flowered, scarcely exceeding the leaves; pedicels 1–2 cm. long, somewhat sparsely appressed-pubescent; sepals obovate-oblong, ciliate on the margin above, 5 mm. long; petals yellow, 8–10 mm. long, glabrous; longer stamens glabrous; styles persistent, very slender, 3–4 mm. long; capsule columnar, 10–15 mm. long, on more or less reflexed pedicels; seeds strongly rugose.

Related to *X. Wrightii**of New Mexico and Arizona, with which it has been confused, but that species is densely villous-pubescent, decidedly glaucous, and has very short, stout styles.

Dry hillsides in the chaparral region of Southern California. Type collected by the author (*3274*) in the Onofre Mountains, San Diego County, April 19, 1903.

Malvastrum viscidum sp. nov.

Annual or possibly sometimes more persistent, 5–10 dm. high; herbage short-stellate-pubescent throughout, somewhat ferruginous, viscid-glandular and heavy-scented; leaves on petioles 15–20 mm. long, nearly orbicular, deeply cordate, 2–4 cm. broad, coarsely crenate; veins prominent beneath; upper surface rugose, appearing almost glabrous; flowers in interrupted spicate clusters; calyx campanulate, 5–7 mm. broad, its lobes broadly lanceolate, slightly acuminate, about equaling the tube; petals reddish, turning purple with age, 15 mm. long; styles pubescent at base, 9 mm. long, equaled by the stamens; immature carpels pubescent at apex, not reticulate on the sides.

A close relative of *M. densiflorum* S. Wats., but much less villous and more glandular; leaves less deeply lobed, and calyx-lobes much shorter. Type collected by the author (*3528*) on dry hill-

* **Xanthoxalis Wrightii** (A. Gray). *Oxalis Wrightii* A. Gray, Pl. Wright. 1: 27. 1852.

sides near El Nido, San Diego County, May 19, 1903. Nevin's specimen from San Juan Capistrano, which Watson referred to *M. densiflorum*, belongs here.

TRICHOSTEMA PARISHII Vasey, Bot. Gaz. 8: 173. 1880

T. lanatum var. *denudatum* A. Gray, Syn. Fl. 2: 459. 1886.

According to Vasey this "differs from *T. lanatum* in the shorter and broader leaves, longer and more slender thyrsus, with cymules more open and much less woolly; flowers smaller and filaments shorter." Dr. Gray simply states "with the wool remarkably short." In all the specimens examined the flowers were scarcely half the size of *T. lanatum*, and the wool much less conspicuous.

T. lanatum ranges from Monterey County to Orange County. In the southern portion of its range it is confined to the foothills toward the coast. *T. Parishii*, according to specimens at hand, is confined to the dry interior foothills, extending over to the desert slopes. It ranges from Acton, Los Angeles County, to the Mexican boundary, and probably southward into northern Lower California.

Gutierrhezia bracteata sp. nov.

Suffrutescent, much-branched above, about 6 dm. high; branches slender, strongly striate, granular-scabrous; leaves at flowering time few, becoming reflexed, 1 mm. wide, 15–40 mm. long, very sparsely short scabrous, obscurely punctate, those of the strictly divaricate branchlets rather numerous, short and bract-like; heads solitary, terminating the ultimate branchlets; involucres turbinate-campanulate, 5 mm. high; involucral bracts in 3–4 series, obovate, very obtuse, with greenish tips; rays usually 8, nearly 2 mm. broad; disk-flowers 7, 4 mm. high, including the achene; pappus-scales obtuse, finely striate, ciliate on the margin.

This species is easily separated from all other members of the genus by its decidedly divaricate, bracted branchlets. Its affinities are perhaps with *G. divergens* Greene, from which it is distinguished not only by the character of its branchlets but by its larger and broader heads.

Desert slopes of San Bernardino County, between Banning and Seven Palms, *C. R. Orcutt*, Nov. 1889. Type in the Gray Herbarium of Harvard University.

STANFORD UNIVERSITY, CALIFORNIA.

INDEX TO AMERICAN BOTANICAL LITERATURE

(1906)

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in its broadest sense.

Reviews, and papers which relate exclusively to forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included, and no attempt is made to index the literature of bacteriology. An occasional exception is made in favor of some paper appearing in an American periodical which is devoted wholly to botany. Reprints are not mentioned unless they differ from the original in some important particular. If users of the Index will call the attention of the editor to errors or omissions their kindness will be appreciated.

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Allison, A. Notes on the winter birds of Hancock County, Mississippi. The Auk **23**: 44–47. Ja 1906.

The vegetation of the county is discussed briefly on pages 44 and 45.

Baillie, A. G. Bog plants. Bull. Pictou Acad. Sci. Assoc. **1**: 23, 24. N 1906.

Baker, C. F. Informe del Departamento de Botánica. Inf. An. Estac. Cent. Agron. Cuba **1**: 131–145. 1 Je 1906.

Baker, C. F. José Blain. Inf. An. Estac. Cent. Agron. Cuba **1**: 217–223. *pl. 30.* 1 Je 1906.

Borge, O. Algen aus Argentina und Bolivia. Ark. Bot. **6**[4]: 1–13. *f. 1–5.* 16 Jl 1906.

Cermenati, M. Ulisse Aldrovandi e l'America. Ann. di Bot. **4**: 313–366. 20 S 1906.

Christ, H. Die *Botrychium*-Arten des Australen Amerika. Ark. Bot. **6**[3]: 1–6. *f. 1–9.* 9 Je 1906.

Includes *B. Negeri* sp. nov.

Cockerell, T. D. A. The alpine flora of Colorado. Am. Nat. **40**: 861–873. 19 D 1906.

Cockerell, T. D. A. The bees of Florissant, Colorado. Bull. Am. Mus. Nat. Hist. **22**: 419–455. 17 D 1906.

Includes a flower-visiting record, in which (!) is published the new combination *Hymenoxys ligulaeflora*.

Cook, M. T. Informe del Departamento de Patología Vegetal. Inf. An. Estac. Cent. Agron. Cuba **1**: 147–207. *pl. 24–29.* 1 Je 1906.

Cook, M. T. Teratología de la piña. Inf. An. Estac. Cent. Agron. Cuba **1**: 242–246. *pl. 43–46.* 1 Je 1906.

Davidson, A. A revision of the western mentzelias. Bull. So. Calif. Acad. Sci. **5**: 13–18. 30 Ap 1906.

Dietel, P. Monographie der Gattung *Ravenelia* Berk. Beih. Bot. Centralb. **20**^{2}: 343–413. *pl. 5, 6.* 1906.

Recognizes 81 species, including 6 North American ones.

Dusén, P. Beiträge sur Bryologie der Magellansländer, von Westpatagonia und Südchile. IV. Ark. Bot. **6**^{8}: 1–40. *pl. 1–12.* 4 S 1906.

Includes 23 new species in 8 genera.

Earle, F. S. Algunos hongos cubanos. Inf. An. Estac. Cent. Agron. Cuba **1**: 225–242. *pl. 31–42.* 1 Je 1906.

Includes new species in *Pocillaria* (5), *Phyllotus* (2), *Geopetalum* (2), *Crepidotus*, *Galera* (3), *Gymnochilus* (5), *Stropharia*, (2), *Pholiotina*, and *Pholiota*.

Foslie, M. Algologiske notiser, II. Kgl. Norske Vid. Selsk. Skr. **1906**^{2}: 1–28. [D] 1906.

Includes new American species in *Lithothamnion* (7), *Archaeolithothamnion*, *Litholepis*, *Lithophyllum* (2), and *Mastophora*.

Fries, R. E. Zur Kenntnis der Phanerogamenflora der Grenzgebiete zwischen Bolivia und Argentinien. II. *Malvales.* Ark. Bot. **6**^{2}: 1–16. *pl. 1, 2.* 9 Ap 1906.

Includes new species in *Bombax*, *Malvastrum*, *Sida*, *Gaya*, and *Wissadula*.

Fussell, L. List of Delaware County plants. Proc. Delaware Co. Inst. Sci. **2**: 34–46. O 1906.

Delaware County, Pennsylvania.

Grant, G. B. *Wheelerella.* Bull. So. Calif. Acad. Sci. **5**: 28. 30 Ap 1906.

Hackel, E. Gramina cubensia nova. Inf. An. Estac. Cent. Agron. Cuba **1**: 409–412. 1 Je 1906.

New species in *Paspalum* (2) and *Leptochloa*.

Hasse, H. E. Contributions to the lichen-flora of Southern California. Bull. So. Calif. Acad. Sci. **5**: 38–45. 11 S 1906.

Hasse, H. E. A few lichens picked up on San Jacinto Mountain. Bull. So. Calif. Acad. Sci. **4**: 123–125. 5 F 1906.

Hemsley, W. B. On the *Julianiaceae*, a new natural order. Jour. Bot. **44**: 379–384. N 1906.

Holm, T. *Ceanothus americanus* L. and *ovatus* Desf.; a morphological and anatomical study. Am. Jour. Sci. IV. **22**: 523–530. *f. 1–5.* D 1906.

Holm, T. The root-structure of *Spigelia marilandica* L., *Phlox ovata* L., and *Ruellia ciliosa* Pursh. Am. Jour. Pharm. **78**: 553–559. *f. 1–5.* D 1906.

Jennings, O. E. A new species of *Lonicera* from Pennsylvania. Ann. Carnegie Mus. **4**: 73–77. *pl. 20.* D 1906.
L. altissima sp. nov.

Kneucker, A. Bemerkungen zu den "*Gramineae* exsiccatae" XXI und XXII Lieferung 1906/07. Allgem. Bot. Zeits. **12**: 178–182. N 1906; 202–205. D 1906.

Landreth, B. A case of persistent vitality in seeds. Proc. Am. Phil. Soc. **45**: 5–8. Je 1906.

Lloyd, C. G. Mycological notes. **21**: 245–260. *pl. 70–73 + f. 88–97.* Ap 1906; **22**: 261–276. *f. 98–123.* Jl 1906; **23**: 277–292. *pl. 86–90 + f. 124–130.* Au 1906; **24**: 283–308. *pl. 91–93 + f. 131–143.* D 1906.

Lloyd, C. G. The *Tylostomeae.* 1–28. *pl. 74–85 + f. 1–6.* Cincinnati, Ohio. F 1906.

Moore, C. L. "Rusts," — with notes on some Nova Scotian species. Bull. Pictou Acad. Sci. Assoc. **1**: 20–22. N 1906.

Palmer, T. C. Rare local ferns. Proc. Delaware Co. Inst. Sci. **2**: 34–46. O 1906.

Parish, S. B. *Cereus giganteus* in California. Bull. So. Calif. Acad. Sci. **4**: 122. 5 F 1906.

Parish, S. B. A preliminary synopsis of the Southern California *Cyperaceae.* Bull. So. Calif. Acad. Sci. **4**: 126–133. 5 F 1906; **5**: 20–28. 30 Ap 1906; [35–37,] 47–54. 11 S 1906.

Pearl, R. Variation in the number of seeds of the lotus. Am. Nat. **40**: 757–768. *f. 1–4.* 26 N 1906.

Perrédès, E. F. London botanic gardens. Am. Jour. Pharm. **78**: 317–325. Jl 1906; 353–365. *pl. 26–30.* Au 1906.

Robinson, B. L. *Oxalis corniculata* and its allies. Jour. Bot. **44**: 386–391. N 1906.

Simmons, H. G. The vascular plants in the flora of Ellesmere-land. 1–198. *pl. 1–10.* Kristiania, 14 My 1906.
Includes a description of *Poa evagans* sp. nov.

Slade, H. B. Studies in plant mutation. Am. Jour. Pharm. **78**: 311–317. Jl 1906.

Van Tieghem, P. Sur les Héliotropiacées. Ann. Sci. Nat. Bot. IX. **4**: 261–271. D 1906.

Viguier, R. Recherches anatomiques sur la classification des Araliacées. Ann. Sci. Nat. Bot. IX. **4**: 1–208. Jl 1906; 209, 210. D 1906.

Warnstorf, O. Neue *Sphagna* aus Brasilien. Beih. Bot. Centralb. **20**[2]: 128–130. 1906. [Illust.]

Description of 7 new species and 1 new variety.

Wheeler, W. M. An ethological study of certain maladjustments in the relations of ants to plants. Bull. Am. Mus. Nat. Hist. **22**: 403–418. *pl. 63–68.* 17 D 1906.

Whitfield, R. P. Notes on some Jurassic fossils from Franz Josef land, brought by a member of the Ziegler Exploring Expedition. Bull. Am. Mus. Nat. Hist. **22**: 131–134. *pl. 18, 19.* 26 My 1906.

Mentions a few fossil plants.